Vol. 21 No. 10

December, 1955

THE BOTANICAL REVIEW

Interpreting Botanical Progress

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ON INSIDE BACK COVER

Published Monthly except August and September
Box 749, Lancaster, Pa.

Entered as second-class mail matter February 4, 1935, at the Post Office at Lancaster, Pennsylvania, under the Act of March 3, 1879.

THE BOTANICAL REVIEW

Founded in 1935 by
HENRY ALLAN GLEASON and EDMUND H. FULLING
Managed, edited and published at
The New York Botanical Garden
by
EDMUND H. FULLING

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THE BOTANICAL REVIEW is published monthly except August and September. Subscription rate for all countries is $6.00; single copies 60¢. All subscriptions are payable in advance at par in Lancaster, Pa., or New York. Checks should be made payable to THE BOTANICAL REVIEW.

Articles are obtained primarily by invitation. Unsolicited manuscripts are also welcome. In all cases, however, the editor reserves the right to accept, reject or suggest revisions in submitted material. All manuscripts should be on double-space typewritten pages, with references and citations in accordance with the customary style of THE BOTANICAL REVIEW.

Missing numbers can not be supplied unless notice is received within two months after appearance of issues concerned.

All correspondence should be addressed to THE BOTANICAL REVIEW, at Box 749, Lancaster, Pa., or Fordham P. O., New York, N. Y.

THE BOTANICAL REVIEW

VOL. XXI DECEMBER, 1955 NO. 10

DWARF MISTLETOES [1]

JOB KUIJT [2]

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[1] Manuscript received Aug. 9, 1955. Joint contribution from the Department of Biology and Botany, University of B. C., Vancouver, B. C., and (Contribution No. 228) from the Forest Biology Division, Science Service, Canada Department of Agriculture, Ottawa, Ontario.

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INTRODUCTION

The genus *Arceuthobium* (Loranthaceae) is one of the most extraordinary genera of flowering plants as well as one of economic importance, for many of its members, commonly known as " dwarf mistletoes ", are significant pathogens of timber trees. Botanically it is distinguished by many uncommon, if not unique, features. Among these may be mentioned the nature of the endophytic system, the female and male flowers, the complexity of the fruit and the ability to induce the formation of witches' brooms on hosts. Economically the damage done by these parasites to many forest trees, especially in western North America, exceeds that of almost any other single cause, with the possible exception of heart-rotting fungi.

It is therefore surprising to find that many of the species have been quite inadequately studied. It is with the possibility of future studies in mind that the present literature review of the genus is attempted.

The writer has collected in excess of 400 references on dwarf mistletoes. For the present, however, only those references were abstracted which, in the writer's opinion, make a definite contribution to a wider knowledge of the dwarf mistletoes. Only these

are listed in the "Literature Cited". Furthermore, and largely because of the unsettled state of classification within the genus, a taxonomic treatment is deferred to a later date, although an outline is indicated in the contents. For a taxonomic treatment of the North American species, the reader is referred to Gill (1935).

MORPHOLOGY AND ANATOMY

Endophytic System

The part of the mistletoe plant developing within the host tissues has been variously named, the particular term used in each case depending upon the writer's idea as to its homology. Thus it has been called a system of rhizomes (von Schrenk, 1900), roots (Heil, 1923; Peirce, 1905; Weir, 1916*a*), thallus (Heinricher, 1923), and finally the endophytic system (Thoday and Johnson, 1930).

Peirce (1905) considered the endophytic system homologous to a true root, originating from a true but modified radicle. From this standpoint he regarded the formation of a shoot as "an instance of regeneration without wounding, amputation or other pathological stimulus". In his view, "the small part of the seedling which penetrates the host forms and develops stem and leaves, a small part of one organ—the root—develops into a complete plant by forming the missing members".

Heinricher (1923), after a series of morphological studies on *Arceuthobium oxycedri*, finally rejected the morphological concept of a root in *Arceuthobium* altogether. He regarded the entire plant as the direct outgrowth of the hypocotyl, neither radicle nor plumule being differentiated in the seedling. Although he believed the endophytic system to be analogous to a root system in function, he thought it more comparable to the mycelium of a fungus, and designated the endophytic system as thalloid. This term, however, is certainly not satisfactory for various reasons, e.g., tracheary elements are present. In view of the lack of agreement as to terminology, the writer prefers to use the non-committal term "endophytic system" suggested by Thoday and Johnson (1930).

The method of entrance of the "haustorium" and the advance of the endophytic system in the host tissues have been matters of considerable debate. The presence of mechanical force is generally agreed upon. There has been some question as to the possibility

of enzymatic action. Heinricher (1923) thus comes to the conclusion that penetration takes place almost exclusively by a forcing aside of the host cells, although he still considers the possibility of secretion of pectase for dissolution of the middle lamellae. Thoday and Johnson (1930) believe that cells of young invading strands have the ability to secrete a wall-softening enzyme, possibly a pectase. Heil (1923) states that cells of the endophytic system dissolve the walls of the host cells, while stone cells are enclosed and digested. Peirce (1905) also speaks of dissolution of host cells by haustorial cells of the parasite.

The anatomy of the endophytic system defies adequate description. The direction of growth of mistletoe strands appears completely erratic except in wood rays, the direction of which is adopted by invading parasitic strands, and in cases where a leaf trace may be followed for a short distance. The young strands are simple filaments of somewhat elongated cells filled with dense protoplasm, each with a large conspicuous nucleus. These filaments branch freely and irregularly, often anastomosing in the manner of a fungous mycelium. The youngest part of the endophytic system contains a stainable substance which later increases slightly in amount. Heinricher (1923) believed this substance to be chlorophyll, but Heil (1923) interpreted it as an oil. These opinions are not necessarily contradictions, since these workers studied different species on different hosts. The remarkable speed of growth of young strands is mentioned by several workers. Thoday and Johnson (1930) found slender strands to within two millimeters of the shoot apex of the host branch in August; the parasitic strands thus seem to keep pace with host elongation. It is probable, however, that the rate and general direction of growth differ from species to species, and perhaps also depend on the species of host involved. *Arceuthobium douglasii*, *A. pusillum* and frequently *A. americanum* seem to grow toward the tips of host branches only, while members of the *campylopodum-vaginatum* complex are able to grow in both directions. These differences in behavior are believed by Gill (1935) to be linked more with the host species than with inherited characters of the mistletoes.

In due course the cells of the young uniseriate strands undergo divisions, at least the first two of which are longitudinal (Thoday

and Johnson, 1930). Thus a series of tiers of four cells each frequently results. During further development a cylinder of cells is formed, the inner cells of which soon begin to differentiate into tracheary elements. The entire process, however, is quite irregular. A continuously functioning cambial layer as well as indications of phloem tissues seem completely absent. Before the cortical strands have fully matured, the first young radial sinkers are already present in the wood.

Observers generally agree that no true phloem is present in either stem or endophytic system of *Arceuthobium,* although the parenchyma surrounding the xylem elements in the latter could be interpreted to represent phloem tissues (Dufrénoy, 1936). Peirce (1905) found this parenchyma in contact with the cells of the host phloem. The association of the xylem tissues of host and parasite has been interpreted variously. Cohen (1954) could observe no direct contact between the xylem elements of *Pinus ponderosa* and those of *A. campylopodum.* Johnson (1888), however, who worked with *A. oxycedri* on *Juniperus* sp., believed that the walls of the host tracheids were separated along the middle lamella through penetration by the parasite. The thin-walled parasitic cells would thus be brought into intimate contact with the host tracheids. Dufrénoy (1936) observed extreme fragmentation of the vacuoles of cells in contact between the two organisms, and accepted this as evidence of active translocation of nutrients.

The gross anatomy of the endophytic system is also characterized by its complexity. Two main types of strands may nevertheless be recognized, cortical strands and sinkers (Solms-Laubach, 1867). The cortical strands occur in the tissues external to the cambium. They have essentially the protostelic features as described above. The sinkers develop endogenously (in *A. campylopodum*) from cortical strands (Cohen, 1954). After penetrating the sheath of the cortical strand, a young sinker, which does not have the tiered arrangement of a young cortical strand, grows centripetally, and usually contiguous to one of the numerous uniseriate phloem rays of the host, until the cambium is reached. No cambium cells appear to be destroyed by the invading strand. A pathological stimulus, however, seems present, causing the cambium to initiate locally a ray which differs markedly in appearance from

both the normal uniseriate rays and fusiform rays containing resin canals. This aberrant ray is formed around the young sinker, which gradually becomes embedded. The embedded sinker constitutes the innermost part of the endophytic system, and seems to maintain a more or less constant position. Scalariform tracheary elements are differentiated in the central zone of the sinkers, but in a very irregular fashion and, according to Heil (1923), not infrequently in contact with host tissues. Clusters of pits form a lattice-like pattern on the side walls of the parenchyma cells of the sinker. Two to several of the aberrant rays may coalesce and form a single large, fusiform, aberrant ray. Within such a compound ray, the original groups of tracheary elements usually remain distinct.

An interesting question is how, or whether, the cortical strands retain their relative position and connection with the sinkers under the constant pressure of newly formed host cells. The distance between the cortical portion of the endophytic system and the sinkers must become greater with time because of the phloem and xylem cells produced by the host. Cohen (1954) suggested some possible explanations for the ability of the mistletoe to cope with this situation. First of all, host cells may, when under pressure, glide past the relatively stationary cortical strands. Secondly, new strands and sinkers may be formed continuously by the inner part of the endophytic system, the large outer strands being discarded with the bark. Cohen also observed some intercalary addition of cells at the base of the sinker which may accommodate the increasing tension in the sinker. It is unlikely that there is any radial movement of the sinkers, for Heil (1923) found a certain coincidence of wall topography in contiguous host and parasite cells: the bordered pits of the host were situated opposite the unthickened parts of the mistletoe xylem elements in the cases where these cells were in contact. The same writer also noted that the cortical strands were not situated parallel to the cambial cylinder of the host, but gradually approached this at their tips. This again could be interpreted to mean that the centrifugal movement of the cortical strands at the oldest part of the infection had been initiated.

The largest cortical strands fuse and separate as irregularly as the youngest filaments. Thoday and Johnson (1930), however,

found two well-developed tendencies in *A. pusillum* on *Picea*. On branches from witches' brooms, the end of each year's growth showed a large number of cortical strands. A cluster of aerial shoots was often present here. Also, at the base of other aerial shoots there was a convergence of strands.

The place of formation of an aerial shoot can first be recognized by a slight swelling on the outer side of one of the largest strands. The tiered arrangement of cells within the strand is lost soon afterwards. The fact that buds always arise on the outside of strands may be attributed to the influence of light. The formation of a bud may be considered analogous to the origin of an adventitious bud upon a root.

Whether the endophytic system is for any length of time dependent upon the aerial parts of the parasite is a question of some interest. Gill (1935) states that strong evidence exists that old infections of *A. vaginatum* and *A. campylopodum* may become systemic in character. They may live for some years within that part of the host where thickness of the bark prevents emergence of shoots, without visible evidence of their presence, until its growth reaches a younger part where profuse fruiting may take place.

Stem and Leaves

A young stem consists of a series of conspicuously articulated segments placed end to end. The basal portion of a segment is usually four-angled; the terminal portion an expanded rounded rim with the vestiges of two decussately arranged scale-leaves that are often indistinguishable from the segment proper. The tendency for roundness of the stems is more marked in some species than in others (Gill, 1935), the taxonomic significance of this is not fully known. Very old basal segments of some species are almost cylindrical, but their shape seems to be a response, in part, to the amount of moisture in the shoot.

The size of the shoot differs greatly between and to some extent within species. Shoots range from a few millimeters (*A. minutissimum*; Gorrie, 1929) and a few centimeters (*A. douglasii*, *A. pusillum*) up to ten and 15 centimeters (*A. vaginatum*, *A. campylopodum*, *A. americanum*; Gill, 1935). While the smaller species can frequently be identified in this way, size alone is unreliable for identi-

fication in the larger species. Thickness of shoots varies similarly, only some smaller species, for example, *A. douglasii,* being readily distinguished by very slender branches. The ratio of length to diameter of segments seems to hold some promise as a segregating character, although this ratio often differs between basal and terminal segments on one shoot. Elongation of the young segment is maintained for several months by intercalary growth; periodic increases in the length of the shoot are effected through the activity of terminal and lateral buds.

Stem color varies from very dark purplish-brown in *A. pusillum* through yellow to bright green in *A. campylopodum.* Eames (1903) found recognizable differences in both color and shape between plants of *A. pusillum* on spruce and tamarack. Other authors suggest that the color of the stem is influenced by such variables as light, temperature and latitude. It is also possible that the physiological state of the host has some effect in this connection (Gill, 1935).

It is only in the larger dwarf mistletoes that branching occurs regularly, though occasionally primary side branches are formed in *A. douglasii,* and rarely so in *A. pusillum.* Two main types of branching may be recognized: verticillate, as in *A. americanum,* and branching in a fan-like manner, as in *A. campylopodum* (Gill, 1935).

The anatomy of the stem is distinct from that of the rest of the Loranthaceae. The arrangement of vascular bundles is to some extent dependent upon the position and age of the section studied (Gill, 1935). In a young fully elongated segment there is one central cylinder of vascular tissue in the middle of the segment, running out into two distinct masses at the distal and proximal ends. With increasing age the number of strands becomes greater and their distribution more scattered. Spiral thickenings make the vessel elements particularly conspicuous. No true phloem has been found, but in old stems there may be a narrow band of thin-walled cells in such a relation to the xylem bundle as to suggest a collateral ectophloic bundle. In young stems even this indication is apparently absent.

The vascular bundles are embedded in a parenchymatous sheath bounded by an uniseriate epidermis. The cells of the sheath retain considerable meristematic qualities. Thus they may pro-

duce, often without much regularity, vascular tissues, strands of sclerenchyma and nests of sclereids. Normal cork is absent from the stems, except where wound cork has been formed.

In young stems a one-layered epidermis is present with stomata, the axes of which are at right angles to the long direction of the stem. The latter feature is likely a result of the intercalary growth already mentioned, and is also found in the other mistletoes. With age, this original epidermis is gradually replaced by a secondary cuticularized layer (Damm, 1901) which is a product of the outer cortical cells. An old shoot, therefore, is supplied with a perennial epidermis-like layer without lenticels or stomata.

The distribution of shoots on host branches may be separated into two general types, although one species, *A. americanum,* may show both types of behavior, even on the same tree (Gill, 1935). Shoots may arise in tufts from small localized centers, as is commonly the case in *A. campylopodum,* or they may be fairly regularly distributed along the length of young branches, which is the rule in *A. pusillum.* The latter has been described by Jack (1900) and Pomerleau (1941). The last year's growth of branches of a mistletoe broom on spruce were found to be without external evidence of the parasite. The second last year's growth showed small buttons of one to two millimeters; the preceding year bore the first shoots and pre-formed flowers. Four-year-old growth supported fruiting branches, after which few shoots were present. Thoday and Johnson (1930) offered a similar description but pointed out the frequent clustering of stems toward the end of the year's growth. This has also been noted for *A. douglasii* (Tubeuf, 1919). Gill (1935) believes that the distribution of mistletoe stems over host branches is primarily a function of the host.

Mention of sterile shoots of dwarf mistletoes is contained in several places in the literature. Johnson (1888), however, found no purely vegetative shoots. Later, Gill (1935) confirmed this when he found "no plants . . . in which all ramifications of the stem were not potentially able to produce at least one crop of flowers. In fact, the shoot has become so expressly modified for reproductive purposes that it might very well be regarded as an inflorescence".

The result of isolated observations without study of the complete life cycle is strikingly illustrated by the inconsistency of the

references to the longevity of dwarf mistletoe shoots. Thus Peirce (1905) and Korstian and Long (1922) believe that shoots of *A. campylopodum* die and are dropped after seed discharge and flowering in female and male plants, respectively. Heinricher (1918) believes the above authors to be incorrect and suggests that insect attack may be responsible. The longevity of the shoots, however, seems to be different for many species. In *A. minutissimum*, shoots are annual (Gorrie, 1929); those of *A. pusillum* are practically biennial (Jack, 1900), attaining their full size in one season, flowering and fruiting in the next, after which they fall away. Dowding (1929) believes that the aerial shoots of *A. americanum* survive several years and produce several crops of flowers. Heinricher (1918) believes the same to be true for *A. oxycedri*. For the remaining species no accurate observations are available. A simple approach to this problem was suggested by Heinricher who noted secondary growth in basal segments of *A. oxycedri* (although no regular annual rings were observed) as evidence of the age of the shoot. It should be relatively simple to apply this method to other species.

As already mentioned, the vestigial leaves can hardly be distinguished from the remainder of the segment. Their arrangement is decussate, and their shape varies from slightly to markedly cuspidate, the slight notches between them sometimes becoming fairly deep sinuses. These features become increasingly obscure with age (Gill, 1935). The stomata, epidermis and cuticle of the leaves seem little different from those of the stem, although Tubeuf (1919) ascribes to the stomata a more active participation in respiration.

Male Flowers

The genus shows some pronounced differences in the time of flowering. No reference regarding the flowering time of any of the Asiatic species could be found. The flowering time of the European *A. oxycedri* has been variously stated as April to May (Klekovski et al., 1869) and August to September (Willkomm et Lange, 1870). Heinricher (1915*c*) offered as solution for this apparent contradiction the suggestion that the flowering time in this species is not definitely restricted, so that single flowers may occur

throughout the year. A distinct maximum was found, however, in September and August.

The North American species can readily be divided into two main groups, one containing those species flowering in spring and early summer, the other consisting of those species flowering in late summer and fall. In the first group belong *A. americanum*, *A. douglasii* and *A. pusillum*. The *A. campylopodum*-complex makes up the second group. The remaining species, *A. vaginatum*, seems somewhat more indefinite in its flowering time, but has a maximum in May and June (Gill, 1935). It is interesting that the latter species is currently separated from *A. campylopodum* only by a two- or three-months difference in flowering time, no consistent morphological differences having been discovered.

Although, again, data from the Asiatic species are lacking, the remaining species show a remarkable uniformity in the morphology of the male flower. If any differences are present they are in degree, not in form, and of no diagnostic value. This seems to apply equally well to the size and shape of individual structures and to color of the flower.

The buds of male flowers share this uniformity to an equal extent, with the solitary exception of the pedicelled habit which seems restricted to *A. americanum* and *A. douglasii* (Gill, 1935), in the latter of which it is rare. The color of the buds varies within the same limits as that of the stem, their shape being dependent to some extent on the position on the shoot. Terminal buds are often globose, those formed in the axils frequently flattened, especially in *A. campylopodum*.

The gross structure of the mature male flowers is extremely simple. Each consists of one whorl which is usually 3-partite, occasionally 4-partite, rarely 2- or 5-partite, each segment bearing a single sessile anther, and joining below a slight elevation of the receptacle, usually termed the "central cushion". From the writer's experience it seems likely that the proportion of 3- and 4-partite flowers may differ between certain species, particularly between *A. campylopodum* and *A. americanum*[3]. This was also

[3] It is of some interest that Mason (1934) also noted a high proportion of 4-partite flowers in fossil dwarf mistletoes from the Pleistocene, which were referred to *A. campylopodum*.

suggested by Dowding (1931*a*) who detected only 4-partite flowers on branches of *A. campylopodum* f. *tsugensis*. Gill (1935), however, states that this can be found in all species.

The shape of the perianth lobes varies from broadly to narrowly or acutely ovate, and from flat to boat-shaped. Their shape is somewhat influenced by the partition, and by position of the flower; terminal flowers are usually more regular. The color of the lobes ranges from greenish to straw color and bright yellow, but may be subject to environmental influences. The entire perianth is shed after flowering.

The nature of the anther alone places the genus *Arceuthobium* in a unique position in all angiosperms. In no other flowering plant does the archesporium of the anther take the form of a continuous ring of tissue around a sterile column. This fact was not at first recognized, and the anther was described simply as bilocular or unilocular. Heinricher (1915*b*) suggested that these different interpretations may be based on sections which did or did not go through the central columella, respectively. Although no evidence in favor of this idea was found, the same author nevertheless believed that the continuous archesporium may be the result of fusion of four locules. Dowding (1931*a*), however, working on *A. americanum,* found considerable support for Heinricher's views. The columella in this species is quite variable. It may divide the anther almost completely into two sacs; it may disappear half way up, a new partition arising at right angles; or partitions may give out branches extending to the anther wall. These partitions tend to divide the single archesporium into four parts, and are present in every degree of incompleteness. The anthers of the remaining species have unfortunately not yet been studied.

The archesporium is surrounded first by a tapetal layer, next by two layers of one cell thick each. The outer or epidermal layer, according to Dowding (1931*a*), becomes the fibrous layer, which is another unique feature of the genus.

Complete agreement prevails among workers on various species regarding the absence of vascular bundles leading to the anthers, which are almost completely sessile. To quote Johnson (1888): "The single vascular bundle of the perianth segment on which the stamen occurs makes a slight bend towards the stamen beneath its insertion, and one or two of the vessels may point a little

towards it, but there is no indication of an independent vascular supply in the stamen". It is interesting to mention the observations of the same author on the development of the stamen. The position of a stamen in a very young flower was found to be quite different from that in an expanded flower. The stamen arises as a multicellular lateral outgrowth of the floral axis, independent of the perianth segment, and acquires its final position by intercalation of the lower half of the perianth segment as a belt of tissue common to the stamen and perianth segment.

The structure usually called the "central cushion" is a mass of undifferentiated cells drawn out in corners alternating with the perianth lobes. It has been interpreted as a rudimentary pistil by Eichler (1878), which view was rejected by Heinricher (1915*b*). As support for Eichler's belief, Dowding (1931*a*) found numerous pairs of glandular cells on the central cushion of *A. americanum*, suggesting nectaries. It is of interest to note that in some species of a closely related family, the Santalaceae, a very similar central cushion exists.

Dehiscence of the anther is by an irregular circular slit. The pollen, when fresh, is bright yellow. Although Dowding (1931*a*) mentions the red color of pollen in *A. americanum*, the color in all material seen by the present writer was bright yellow. Individual pollen grains are sphaeroid, with three spinulose lobes separated by three smooth grooves which converge at the poles. Gill (1935) recognized differences in size and shape between specimens. Furthermore, the grains of *A. pusillum* seemed to be consistently larger than those of other species.

Chromosomal work has been done on young anthers only; the results, however scanty, merit mention. Pisek (1924) reports that meiosis in *A. oxycedri* was often interrupted because of physiological difficulties in the nutrition of the parasite; irregularities in the distribution of chromosomes to the tetrad cells may occur, leading to degeneration of pollen in many anthers. According to this author, a relation between the occasional shift in chromosome numbers and pathological difficulties may possibly exist. Diploid and haploid chromosome numbers of this species are believed to be 26 and 13. In other respects, meiosis agreed with that of *Viscum;* sex chromosomes were not distinguishable in either of these species. Dowding (1931*a*) found meiosis in *A. americanum* to occur in

late July, the chromosome number of this dwarf mistletoe being $n = 14$. From material examined by the present writer, this would seem to take place in the middle of August, although this difference may be the result of geographical and seasonal variation. No cytogenetical work has been attempted on any of the remaining species.

Female Flowers

The same uniformity of morphology characteristic of the male flower prevails in the female blossom in all species of *Arceuthobium* studied. Again, data on the Asiatic species are completely absent [4], and so only the female flower of the European and some New World species can be discussed.

A mature flower is a small elliptic structure of the same color as the shoot, and in some species hardly protruding from it (Heinricher, 1915*b*). The perianth consists of two, rarely three, lobes which are almost entirely fused with on another and with the pistil, the style of which is slightly longer than the perianth segments. Within the ovary a single locule contains an undifferentiated mass of tissue, the ovarian papilla, embracing the two embryo sacs.

Thus the morphology of the pistillate flower is such that it does not open in the manner of the male flower. This renders it extremely difficult to judge the length of the flowering season by the female flower alone. It is probably safer to accept as criterion for the flowering time of a species that of nearby male plants (all dwarf mistletoes are dioecious). In contrast to the latter, the flower of the female plant is not shed, but the entire floral organ develops into the fruit.

The 2-partite condition of the pistillate blossom is an important generic character, but in at least two instances 3-partite flowers have been recorded (Gill, 1935). Several shoots of 3-partite pistillate flowers have been found of *A. vaginatum* on *Pinus leiophylla*. Perianth segments of these were bright orange, somewhat divergent from the pistil and united for only half their length. One instance where a trimerous flower had developed into a fruit has been reported from *A. pusillum*. The rarity of these cases,

[4] Datta in 1951 described a highly unusual flower of *A. minutissimum*. This flower was bisexual and 2-partite; the ovary completely superior instead of inferior; and the stigma trifid. These features are so extraordinary that, in the opinion of the present writer, this flower can hardly be interpreted until the floral morphology of this species is better known.

however, still allows the maintenance of the 2-partite conditions as a generic character.

The extreme simplicity of the female flower is in striking contrast to the complexity of the fruit developing from it. The base of each perianth segment is invaded by a vascular strand which branches in a fan-like manner and nearly reaches the tip. Smith and Smith (1943) considered some of these traces to be "recurrent", and from this inferred the inferior ovary in *Arceuthobium* to be of receptacular origin. The carpels, on the contrary, are entirely evascular and are fused with the perianth segments to such a degree that only a very short style and stigma emerge from the mouth-like opening of the perianth. In *A. americanum* the stigma is unequally bilobed. On the basis of shallow indentations in the stigma of this species, Dowding (1931*a*) considered the ovary to consist of four carpels which fuse in varying degrees, in two's and three's. According to this interpretation, three carpels are commonly fused completely, the fourth incompletely, although all four may be fused occasionally, forming a complete rim. No evidence supporting this theory has been put forward for other species. Thoday and Johnson (1930) found slender septate hairs on the stigma of *A. pusillum,* even after shrivelling up of this organ; this has not been reported for other species.

From the stigma an obscurely funnel-form stylar canal, entire or two- to four-lobed, leads down to the single locule. The epidermis of this canal is covered by a thin cuticle. The stigmatic exudations observed by Dowding (1931*b*) and Heinricher (1915*b*) on *A. americanum* and *A. oxycedri,* respectively, are believed to originate in this epidermis. Heinricher thought the exudate of the European species to be a fatty oil, emerging through the stomata of a definite region of the stylar canal. Later this drop would be withdrawn into the flower, simultaneously drawing pollen grains caught in the drop into the stylar canal. If Heinricher's interpretation is correct, another unique feature is added to those of the dwarf mistletoes, for oil as a secretion of the stigma or as a receptive fluid for pollen grains is not known from any other Angiosperms.

The embryo sacs are embedded in a terminal outgrowth of the floral axis consisting of undifferentiated parenchyma enclosed in a columnar epidermis. No suggestion of integuments is present.

By this feature, i.e., the absence of true ovules, the Loranthaceae are separated from the Santalaceae which have a single erect ovule. Within the ovarian papilla the two embryo sacs are situated toward the apex and near the surface. The fact that these embryo sacs alternate with the four carpels, as distinguished by her, led Dowding (1931*a*) to believe that " the four outer carpels are sterile and bear only stigmas, while the embryo sacs are borne on an inner whorl of orthogonally arranged carpel rudiments ". This belief was sustained by the fact that four, not two, groups of archesporial cells are first present in the young ovarian papilla, these groups alternating with the four carpels recognized by the same author. The gynoecium would therefore be represented by: G = 4 + 4.

According to this hypothesis, the ovarian papilla would be a fusion of four rudimentary elements. This, however, is opposed to the view of Johnson (1888) who believed the ovarian papilla to be " a placenta formed of the modified apical part of the floral axis bearing two imbedded ovules reduced to their simplest condition ". Bancroft (1935) also rejected the theory of carpel polymorphism. It must furthermore be kept in mind that the hypothesis of Dowding is entirely based on her interpretation of the stigma of one species, and that no other species have as yet been studied in this respect.

Pollination, Fertilization, Embryology

From the description of the pollen grains of *Arceuthobium* it may be seen that they are more typical of entomophilous than of anemophilous plants. A thorough consideration was given to both possibilities by Heinricher (1915*b*). The only feature which the dwarf mistletoes have in common with many anemophilous plants is the inconspicuousness of the flowers, especially the pistillate ones. Other features usually associated with this type of pollination are completely absent. On the other hand, several entomophilous features are present, among which may be mentioned the sessile anthers, the moderate amount of pollen produced, the spinulose nature of the pollen, making it cling together in balls, and the presence of a stigmatic secretion. Heinricher (1916) found that few berries were produced on plants kept in a greenhouse and concluded that, although insects probably play the most important role in pollination, both types of pollination can occur in nature. Weir

(1915) observed hymenopterous insects taking part in pollination, while the writer has seen ants visiting flowers of male plants of *A. americanum.*

The time elapsing between pollination and fertilization seems to be different for several species. Johnson (1888) found in *A. oxycedri* (presumably flowering in the fall) that the pollen grains sent a thin pollen tube down the stylar canal, which penetrated the ovarian papilla at its summit and passed in for some distance toward the apices of the embryo sacs; then it became dormant until the next spring, when fertilization took place. Dowding (1931*b*), however, observed fertilization taking place a few days after pollination of *A. americanum,* a spring-flowering species. This must occur also in *A. pusillum,* where production of fruit takes place in the same season as pollination. At any rate, macroscopic changes occur in all spring-flowering species directly after pollination, while in all others there is no apparent development until the following spring. Development of the fruit, however, is not always dependent upon fertilization, since fully developed fruits without a trace of embryo or endosperm are not infrequently found (Gill, 1935).

Development of the embryo sac seems to follow the usual pattern in angiosperms. Johnson (1888) saw several intermediate stages leading to the mature embryo sac which, as has been pointed out, is completely embedded in the tissue of the ovarian papilla. Knowledge of the developing embryo is only fragmentary. Thoday and Johnson (1930) believed that no suspensor is formed in *Arceuthobium;* this is also the case in *Viscum.* Nevertheless they did observe a haustorial extension thrust down by the developing embryo into the base of the ovarian papilla. The entire ovarian papilla is pushed aside by the enlarging endosperm and after a few months is to be detected below it. The mature embryo is extremely simple and will be further described in the following section.

In several places in the literature on *Arceuthobium* the occurrence of polyembryony is mentioned. It is false polyembryony, since the two " seeds " are produced by two embryo sacs of independent origin (see Webber, 1940). Peirce (1905) first found two embryos within a single " seed " of *A. campylopodum,* but they were of unequal size, and only one could have developed into

a new plant. Johnson (1888) had previously been unable to find polyembryony in *A. oxycedri.* Weir (1914) observed two embryos in one "seed" in *A. americanum, A. douglasii* and *A. vaginatum* f. *cryptopodum.* No information on the occurrence of polyembryony in any of the other species is available.

Mature Fruit: Dispersal Mechanism and Subsequent Germination of the "Seed"

Because of the selective nature of the present treatment, the large amount of detailed information on the fruit available from several papers cannot be included. The following is based on Gill (1935). For more detailed information and specific differences, the reader is referred to Johnson (1888) and Heinricher (1915*c*) on *A. oxycedri,* to MacDougal (1899) on *A. vaginatum* f. *cryptopodum* and to Peirce (1905) on *A. campylopodum* f. *campylopodum.*

Fruits have been described accurately for only a few species. In general the mature fruit ranges in color from blue to olive green. It is a fleshy, ovoid to oblong structure, attached to the shoot by a recurved pedicel. A striking feature in the genus is that the upper and lower parts of the fruit are invariably of different shades, separated sharply by an equatorial line. Despite the fact that a number of older species, now reduced to synonymy in many cases, were said to be distinguishable on fruit characters, more careful observations appear to indicate that these have little specific diagnostic value (Gill, 1935).

Anatomically the fruit consists of a highly specialized and differentiated pericarp, enclosing an otherwise naked endosperm and embryo. Below the equatorial line the exocarp consists of a thinly cutinized epidermis without stomata. This overlies a layer of parenchyma consisting of irregularly shaped living cells with slightly thickened secondary walls and interspersed with conspicuous intercellular spaces. This layer, which resembles the spongy parenchyma of some leaves, is eight to ten cells thick in the mature fruit. It extends from the equatorial line to the dehiscent layer at the base of the fruit. Inside this spongy tissue is a layer of parenchyma composed of relatively thick-walled, closely packed cells. As pointed out above, the spongy layer ends at the equatorial line, where it is replaced by the sclerenchyma sheath. The epidermis over this sheath is heavily cutinized and provided with stomata.

The only vascular tissues in the fruit are two strands of primary xylem, one median in each perianth segment.

A sheath of mucilaginous cells, dome-like above, encloses the "seed". The cells of this mucilaginous layer, which is thought to correspond to the mesocarp, are elongated, the ends being firmly attached to the exocarp and endocarp. Johnson (1888) found these cells to be filled with viscin, developed through dissolution of the originally extremely thick cell walls.

The endocarp is represented by a sheath of large, angular, thin-walled cells without intercellular spaces. At maturity these cells are crushed, forming an envelope around, but never attached to, the endosperm and embryo.

The straight cylindrical embryo lies in the longitudinal axis of an ovoid mass of endosperm. As pointed out above, true ovules are not present in this genus; consequently we can not speak of seeds as such. The embryo consists of an undifferentiated mass of cells covered by a one-celled columnar epidermal layer, and is slightly notched at the cotyledonary end, but otherwise entire. As Tubeuf (1923) has shown, the radicle is slightly exserted from the endosperm; it lacks a root cap and is distinctly green.

Lack of agreement between authors indicates that the mechanics of the explosive dehiscence of the fruit is still not completely understood. For the present, Heinricher's (1915*c*) and Johnson's (1888) descriptions are followed, but for other interpretations the reader is again referred to the authors mentioned above.

The existence of considerable pressure as the propelling force of the "seed" is, of course, undeniable. Heinricher considered this pressure to be built up in the mucilaginous layer through imbibition of water by the slime threads. He further inferred that the parenchyma layer acted as a water storage tissue for this purpose. At maturity the pressure built up in the fruit is so great that the pericarp gives way at the dehiscent layer at the base of the fruit. The dehiscent zone is torn horizontally, the elasticity of the stretched pericarp comes into play, and the oblong tapering "seed" is shot out through the base of the fruit, often for a distance of over ten yards (Dowding, 1929). At this expulsion the viscid cells are torn across at the distal ends, so that the cell sap escapes. Thus the mucilage is provided by means of which the "seed" adheres to a host branch or other object in its path.

Expulsion of the "seed" takes place in late autumn. Germina-

tion may follow immediately or, more usually, is delayed until the following spring. The radicle grows, often for a considerable distance, along the surface of the substrate until an obstruction is met (Gill, 1935). At the obstruction an irregular mass of undifferentiated cells is formed, the "foot", the nutrients for which are evidently provided by the older portion, as it soon withers and dies off. In the meantime the endosperm has been exhausted by the growing embryo, and some vascularization has begun, first in the radicle, later in the "foot". The "foot" eventually sends down a haustorium-like projection, by means of which a new infection is established. The radicle by this time has completely deteriorated. Any aerial shoots formed in later years are produced adventitiously by the endophytic system and have no direct relation to the embryo.

Ecology of "Seed" Dispersal and Germination

Very little is known about the conditions prompting discharge of the "seed". Many authors allude to certain moisture conditions necessary but fail to provide details. The distribution of one species, *A. pusillum,* was attributed to the high atmospheric humidity associated with coastal regions (von Schrenk, 1900). Further work on this phase of the life cycle is certainly needed before an explanation of the distribution of the parasite can be attempted.

Two other agencies which may aid the distribution of "seeds" are wind and animals. Wind is apparently of some importance or at least is most noticeable in those areas where winds are persistently from the same direction. Here the spread of *A. campylopodum* is clearly most rapid in the direction of the prevailing winds (Weir, 1916*a*; Roth, 1953). The possible role of animals in dissemination has been given somewhat more, though still superficial, attention. Suggestions of a speculative nature are to be found in von Schrenk (1900), Turrill (1920) and Buckland and Marples (1952), where some disjunct distributions of dwarf mistletoes are attributed to transportation of "seeds" by animals. Actual observations of English sparrows and grouse feeding on dwarf mistletoe berries were made by Weir (1916 *a, b*) and of finches and other birds by Gorrie (1929). Birds and rodents frequently build their nests in witches' brooms and so come into contact with the mistletoe plants. All authors, however, agree that the role of wind

and animals in the dissemination of " seeds " is of relatively minor significance.

As mentioned above, germination may begin in the fall or early spring. In the first case, growth of the radicle is often arrested during the cold season and resumed when proper conditions return. Weir (1918*b*) found that a higher percentage of germination was obtained when the " seeds " had undergone freezing temperatures, which fact may explain why most " seeds " in nature do not germinate until spring.

Heinricher made some observations on the germination of " seeds " of *A. oxycedri*. He noted that " seeds " on glass or inorganic material failed to germinate, while those on boards and filter paper did. From this evidence he concluded (1915*a*) that a stimulus went out from organic material (perhaps from cellulose) to effect germination. This view was also held by Palhinha (1942) who states that one of the conditions for germination is " almost certainly " some undetermined chemical stimulus. In a later paper, however, Heinricher (1917) corrected his earlier deductions, after finding that " seeds " germinate on both organic and inorganic substrates, as long as a sufficient supply of liquid water was present. In nature this requirement is possibly met by absorption of large quantities of water by the very hygroscopic mucilaginous layer. Several field observations by other workers (Peirce, 1905) confirm Heinricher's most recent views, viz., that dwarf mistletoe berries may germinate on any object provided moisture conditions are suitable.

An interesting feature of the germinating " seed " is the apparent presence of phototropism and geotropism. As early as 1888 Johnson recognized a distinct curvature of the radicle towards the host branch and assumed negative phototropism to be responsible for this movement. Heinricher (1917) confirmed this for another species and added that negative geotropism may also become evident. Extension of these studies is certainly warranted, where the later work of Tubeuf (1923) on the germination of *Viscum album* will be very suggestive.

It has been held by many workers that dwarf mistletoes can not become established on unwounded host tissues older than three years. Weir (1918*b*) believed this apparent resistance of older tissues to infection to be due to cork formation and the absence of

chlorophyll in the bark. By exposing older tissues which still contained some chlorophyll, he was able to effect establishment on branches up to seven years old. A recent worker, however, has shown that these assumptions can not be made in at least the parasitism of *A. americanum* on *Pinus contorta* (Hawksworth, 1954). This mistletoe was demonstrated to be able to become established through the bark of stems at least 58 years old. Furthermore, dissection of trunk infections indicated that establishment on tissues older than five years was of very frequent occurrence. These facts are of great silvicultural importance, and similar information of other hosts and dwarf mistletoes would contribute much essential knowledge to future control programs.

Physiology

Although no major physiological work has been conducted on dwarf mistletoes, several authors have submitted their ideas on some aspects of this field of study. *Arceuthobium* has been called totally parasitic (Cannon, 1901); it has been claimed that the genus is semi-parasitic, absorbing only water and nutrient salts (Heil, 1923); recent workers, however, regard it as inconceivable that the parasites manufacture all the food which they require (Gill, 1935).

Closely tied up with the question of dependency on the host is the presence of chlorophyll in dwarf mistletoes. Chlorophyll has been reported in several species, e.g., *A. oxycedri* (Heinricher, 1923) and *A. campylopodum* (Peirce, 1905), but not all species seem to be the same in this respect. For example, Heinricher found chloroplast-like bodies throughout the endophytic system of *A. oxycedri,* but Thoday and Johnson (1930) were unable to do so in *A. pusillum.* Many misstatements on the absence of chlorophyll are due to the fact that often brownish pigments in the epidermal cells mask the green tissues underneath. The presence of chlorophyll in the endophytic system seems somewhat problematic, since the light intensity there must be extremely low.

In a previous section it was mentioned that the anatomical evidence, though scarce, points to an absence of ordinary phloem tissue and its typical features. Although sieve plates have not been found to connect sieve tubes of the host and the living cells of the parasite, we are not justified in stating that no elaborated

food is absorbed from the host. Movement of nutrients through the thin separating walls in some places is inevitable because of different concentrations of dissolved food substances.

A feature which is encountered especially where broom formation takes place is the excessive storage of starch in host tissues at the point of infection and even in the endophytic mistletoe cells (Weir, 1918*b*). It is considered a direct result of the excessive flow of nutrients to the parasite. In time, however, a conspicuous starch deficiency develops at the infected parts (Heinricher, 1923), which may be attributable to interference in normal conduction or excessive local development of host branches into a witches' broom.

Most of the *Arceuthobium* species typically occur in dry locations, although some exceptions exist. Nevertheless it is obvious that the extreme morphological reduction is of great value in the many cases where dwarf mistletoes grow under very xeric conditions. Reduction in leaf surface, thickening of the outer walls of the epidermis, and screening of excessive radiation by other pigments are all very evident protective adaptations to conditions which, at least during certain seasons, approach desert conditions.

Meanwhile it must be kept in mind that the primary physiological requirement of a dwarf mistletoe plant is a suitable host. Exactly what determines the suitability of a particular host for a certain species of *Arceuthobium* is not yet known. Marked host affinities and antipathies unquestionably exist, but the extent of these has not been fully explored. Further inoculation experiments are therefore highly desirable.

HOST RELATIONSHIPS

Morphological Effects on Host

Among the economically and silviculturally important features of the dwarf mistletoes are the various aberrations of growth called forth in the host tree. These abnormalities may be divided into three main categories; intergrades, however, are common.

SWELLINGS AND CANKERS

A fusiform swelling on the young branch is frequently the first external evidence of the presence of a dwarf mistletoe. In most host species, infected branches become swollen to some extent. These swellings are due to both an abnormal increase in the pro-

duction of host xylem and phloem and to the mass of parasitic tissue (Heil, 1923). This initial hypertrophy may be followed by the development of witches' brooms, the component branches of which are likely to be conically swollen, i.e., broadest at their base with a marker taper. Infections by *A. campylopodum* characteristically result in such conically swollen branches. When infections involve the trunk of the tree, hypertrophies may develop without brooming. Such infections have serious economic importance and are also of great biological significance, as they undoubtedly shorten the life of the host (Gill, 1935).

Older swellings may eventually show areas of local necrosis. On the bole and large branches, these are often evident by the copious flow of resin from the necrotic area (Korstian and Long, 1922). A cross section of such a "resin canker" usually shows large areas of sapwood infiltrated with resin. This infiltration continues until the fibrovascular system is clogged with resin, killing the limb.

WITCHES' BROOMS

Heinricher (1918) was the first to point out that the ability to induce witches' brooms on host trees places the dwarf mistletoes in a unique position among flowering plants. Many other Loranthaceae grow into broom-like formations. The only other known plants that call forth this unusual growth from the host, however, are some parasitic fungi, for example, *Peridermium coloradense* (Dietel) Arth. and Kern on spruce.

That infection by dwarf mistletoe must inevitably lead to the formation of a witches' broom does not appear to be correct in all cases. The European species, *A. oxycedri,* is only occasionally associated with witches' brooms. The same is true of *A. minutissimum,* where, if brooms develop, they do so especially on dry sites (Gorrie, 1929). The situation in the North American species has not yet been fully analyzed.

Witches' brooms are typically dense masses of twiggy growth, varying greatly in size, even to the extent of involving whole trees (Gill, 1935). Brooms on *Tsuga* are horizontally flattened, those on *Larix* radiate out from a common area of origin, while those on the pines, spruces and Douglas-fir become more or less spherical. With certain reservations, Heinricher's (1918) observations on juniper have general application in North America. First, he

noted a local concentration of secondary branches. Secondly, the infected branches become negatively geotropic, emphasizing the broom-like appearance. A third feature may be added from North American examples, the elongation of individual branches of a witches' broom. That negative geotropism is not always found in brooms is shown by those caused by *A. douglasii* and others, where the branches often droop. Marked negative geotropism was, however, apparent in some North American cases, at least in the initial stages of broom formation (von Schrenk, 1900; Dowding, 1929). The morphological characteristics of a witches' broom, therefore, are partially determined by the nature of the branching in the host.

Occasionally witches' brooms may be several hundreds of pounds in weight (Buckland and Marples, 1952). It is not surprising to find, therefore, that the supporting branch is sometimes thicker than the main stem at their junction. One effect of this continuous weight is a marked eccentricity in annual growth of the supporting limb, more wood being formed in the lower half of the branch (Korstian and Long, 1922). It is also not surprising that brooms of great proportions have a very serious effect on the remaining uninfected part of the tree. In most North American mistletoe hosts, especially in Douglas-fir, "spike top" and similar features are a common sight in areas of infection. In these cases the drain of nutrients imposed by the broom gradually retards the growth of the healthy part to such an extent that the entire tree may be leafless with the exception of the witches' broom.

The best attempt at explaining the causal mechanism of broom formation is in one of Heinricher's publications on *A. oxycedri* (1918). He believed the formation to be related to the distribution of the parasite on the host. Experimentally it was found that *Juniperus,* when infected in only one place, developed a broom, while this did not take place where a large number of infections was present on one plant. The explanation offered for this difference was as follows. A localized infection may cause a flow of nutrients to the seat of infection, where storage of nutrients takes place to such an extent that the formation of buds and their development into branches are induced. When, however, many mistletoe plants are present on a juniper, these compete with one another. Therefore no food storage takes place, as the mistletoe uses all nutrients brought on, no surplus storage being present, no extra

branches or a witches' broom is formed. At once an objection to this theory seems present in the many North American examples where several to many witches' brooms are on a single tree. With some modifications, however, this theory may still hold for at least some of the other species.

OTHER EFFECTS

Aside from the above effects, mature mistletoe infections are usually accompanied by a variety of less tangible features. These have not been quantitatively studied but have much in common with the symptoms of other serious diseases. Some of these features may be mentioned separately.

The leaves of the infected branches, especially of brooms, are commonly distinctly shorter and often lighter in color than those of healthy branches. In *A. americanum* infections, leaves adhered to host branches several years longer than those on healthy ones (Dowding, 1929). In the case of *A. pusillum* the host branches were distinctly but uniformly thicker than normal ones (Thoday and Johnson, 1930).

A decrease of the radial increment of infected trees was determined with certainty in *Pinus ponderosa* (Korstian and Long, 1922), although this is probably a characteristic of most infections. However, an accelerated growth was noted in lightly infected trees, which may be due to a possible stimulating effect, as with minute quantities of many toxic substances.

Silviculturally it is significant that seed production is also influenced by mistletoe infection (Korstian and Long, 1922). With severity of infection there is a marked decrease in the percentage of germination, yield of cones and seed per tree, and consequently in the reproductive value per tree. On the other hand, lightly infected trees may experience a slight stimulating effect. The few cones occasionally on infected trees are often aborted or infested with insects. For these reasons, infected trees left for the purposes of seed production after logging are of very limited value.

Fungus and Insect Attack in Relation to Dwarf Mistletoe

The effect of most serious tree diseases is that the general vigor of the tree is eventually decreased to such a low level that the tree becomes more susceptible to other diseases as well. Mistletoe in-

fections are no exception to this rule, and in several places in the literature the association of mistletoe attack with that of some fungi and insects is recognized.

This increased susceptibility may result from a general decline in vigor or from local wounds in the infected tree. For example, the necrotic areas in mistletoe infections can easily serve as seats of infection, not only for bark- and wood-inhabiting fungi but also for certain insects. Weir (1916*a*) found larvae of the flat-headed fir borer (*Melanophila drummondi* Kirby) in many mistletoe burls. Korstian and Long (1922) found on trees, dead or dying from mistletoe infections, species of secondary bark beetles and borers, such as *Ips, Pityophthorus, Chrysobothris* and *Melanophila.* Also, the few cones occasionally borne on heavily infected trees are frequently infected with a cone insect (*Conophthorus ponderosae*). Significant is the statement of Buckland and Marples (1952) to the effect that healthy western hemlock withstood the effects of successive defoliations by the hemlock looper much better than those with dwarf mistletoe infections. Of a more speculative nature is the report of Korstian (1925) regarding a coincidence of the ranges of certain species of bark beetle and of dwarf mistletoe, and those of their hosts, two types of yellow pine. The significance of this indication, however, can not be fully evaluated until the taxonomic relationships of the dwarf mistletoes concerned are better known.

Secondary attack by fungi may become manifest in various ways. Necrotic areas on mistletoe infections provide an avenue of entrance for fungi, some of which may become established and girdle the branch. This frequently happens on mistletoe-infected branches of *Abies magnifica* in the Sierra Nevada, where *Cytospora* spp. are responsible for girdling (Gill, 1935). When witches' brooms are broken off and when mainstem infections develop into cankers at maturity of the tree, large open wounds are left on the trunk, facilitating the establishment of many of the most serious heart-rotting fungi, such as *Trametes pini* (Brot.) Fr. and *Echinodontium tinctorium* E. and E. (Hedgcock, 1915), eventually making the tree liable to windfall. In western hemlock, Englerth (1942) found that more than 30 per cent of decay in stands in western Oregon and Washington was traceable to mistletoe malformations, while Foster et al. (1954) made similar observations for the upper Columbia region of British Columbia.

Methods of Controlling Parasitism

Workers outside North America have not been concerned with the problem of how to control the destructive dwarf mistletoes. With the possible exception of *A. minutissimum*, which reduces the cover value of *Pinus excelsa* in the Himalayas, the species outside this continent are nowhere of economic importance, and no control is necessary. The importance of North American species has already been touched upon; but few, if any, of the following methods of control have emerged from the hypothetical or experimental stage.

CHEMICAL

The development of a great variety of selective herbicides within recent years has brought up the question whether one can be found to kill dwarf mistletoe without injury to the host. Considering the remoteness of relationship between hosts and parasites, it seems reasonable to expect that one of these selective chemicals might be effective. An initial study of this kind is in progress in Alberta (Bourchier, 1954). A systematic search, however, has not as yet been made. Of considerable interest are the results obtained by Greenham, et al. (1952), who found that trunk injections with 2,4-D showed some promise as control of *Loranthus* spp. on a *Eucalyptus* species in Australia. A full-scale investigation into the possibilities of chemical control of dwarf mistletoe is certainly warranted.

BIOLOGICAL

Biological agents of control may be divided into three groups: hyperparasitism by fungi, feeding by insects, feeding by birds and mammals.

FUNGI. Three fungi have been found parasitic on various species of *Arceuthobium*. None of these parasitic fungi is known outside North America.

The first parasitic fungus described on dwarf mistletoe is probably the most wide spread, certainly the most specific, of the three. *Wallrothiella arceuthobii* (Pk.) Sacc. (Sphaeriales, Ascomycetae) was first found by Peck (1875) on *A. pusillum* in the eastern United States, but subsequently in the West on the following hosts: *A. americanum, A. douglasii, A. campylopodum* f. *abietinum*

and f. *microcarpum* (Gill, 1935). The known range of this fungus in the West is from northern Alberta to Arizona, although quite local in occurrence.

The fungus is unusually specific in its requirements and has not yet been cultured. It attacks pistillate flowers only, allowing all except the inner tissues to develop. At maturity a black stroma and perithecia with club-shaped asci containing dark ascospores develop at the stigmatic region. *Wallrothiella* therefore interferes with reproduction by destroying the "seed". Gill (1935) and Dowding (1931*b*) believe it of no practical consequence as an artificial biological control, particularly since it seems restricted to damp localities. A recent observer (Thomas, 1953), however, has found it commonly in dry localities and believes it to be of more consequence. The parasite was noted by the writer during the summer of 1953 in some very dry localities at Kimberley and Yellowhead Pass, B. C.

The second parasitic fungus on *Arceuthobium* has been known only since 1932. *Septogloeum gillii* Ellis (Fungi Imperfecti) was described by Ellis (1946) who found it to occur on stems (rarely on fruits) of several species. The fungus forms small yellowish-white lesions, often coalescing and erupting irregularly, liberating large masses of hyaline spores. Lesions are often concentrated near the nodes and are most common in summer and fall. Shoots of all ages may be attacked, but there appears to be a preference for pistillate plants. *Septogloeum gillii* has been found naturally on the following dwarf mistletoes: *A. americanum, A. douglasii, A. campylopodum* formae *abietinum, blumeri, cyanocarpum, divaricatum, microcarpum, tsugensis* and *campylopodum. A. vaginatum* f. *cryptopodum* was infected only after inoculation of wounds. Because of its virulent nature, this fungus is believed to have possibilities as a biological control.

The third fungus is known from one locality only, Point Lobos Reserve, California, where it was found on stems and leaves of *A. campylopodum.* It was named and described by Linder (1938) who called it *Metasphaeria wheeleri* Linder (Sphaeriales, Ascomycetae). It girdles stems, killing that portion of the stem beyond the infected area. The stems become yellowish and stand out in marked contrast to healthy brownish-green plants. As a biological control it probably has little value.

INSECTS. Several insects are known to feed upon species of dwarf mistletoe. Most of these are considered of little value in mistletoe control. Weir (1915) reported seeing grasshoppers feeding near Spokane, U.S.A., on yellow pine mistletoe (presumably *A. campylopodum* f. *campylopodum*). Heinricher (1915*c*) found shoots of *A. oxycedri* attacked by thrips. Spittle insects (Cercopidae) were found on *A. vaginatum* f. *cryptopodum* (Korstian and Long, 1922) and *A. campylopodum* f. *campylopodum* (Gill, 1935). Two Lepidoptera, *Mitoura spinetorum* Hew. (Comstock et al., 1938) and *Neoborella tumida* Knight (Knight, 1927), have been observed on *A. campylopodum* and *A. vaginatum* f. *cryptopodum*.

Of these insects spittle bugs are probably the most destructive to dwarf mistletoe plants. They mine out stems, causing death of the entire shoots. In some cases heavy mortality was noted (Gill, 1935). Older shoots were attacked primarily, and a partial check on reproduction may thus be imposed.

That more mistletoe-feeding insects exist seems very probable. The writer found larvae of an insect in stems of *A. campylopodum* f. *tsugensis* in the Botanical Gardens at the University of British Columbia, Vancouver, Canada. Stems were mined out completely, thereby killing the remainder of the shoot.

BIRDS AND MAMMALS. The interrelationships between dwarf mistletoes and vertebrate animals are very inadequately known; this is shown by the fact that only four brief references to vertebrates were located in the dwarf mistletoe literature. Weir (1916*a*) listed mistletoe berries and plants in the stomach of grouse, and observed English sparrows feeding on berries, which evidence is unequivocal and has its implications in the distribution of mistletoe "seeds". Some rodents are known to prefer the swellings on mistletoe infections, and infected branches often show the signs of feeding by squirrels and porcupines (Korstian and Long, 1922; Taylor, 1935). Their preference for this spongy cortical mass may be attributable to the abundance of starch in such infections (Dufrenoy, 1936).

SILVICULTURAL

Attempts at silvicultural control have been directed mostly at the inhibition or restriction of normal "seed" distribution. Cer-

tain field observations provide a basis for possible control. The findings of Buckland and Marples (1952) may be mentioned first. Working with the hemlock mistletoe (*A. campylopodum* f. *tsugensis*) on western hemlock, three methods of logging were applied, and the resulting effect on the occurrence of the parasite observed. Where extensive clear-cutting took place, the subsequent reproduction showed mistletoe in some widely scattered locations only. Where only occasional trees or scattered blocks had been left, the mistletoe had rarely spread far into the reproduction. These trees did, however, serve as well-established centers of infection. Finally, where selective cutting was practiced, mistletoe was present throughout the new stand.

It is a well-recognized fact that the greatest spread of dwarf mistletoe is from overstory to understory (Gill and Andrews, 1942; Anderson and Kaufert, 1953; Roth, 1953). Uneven-aged stands are therefore more severely attacked than comparable even-aged ones. Also, mistletoe grows more rapidly after a part of the stand has been logged off, apparently because of improved light conditions (Korstian and Long, 1922). It is evident, therefore, that selective cutting ("high-grading") of a mistletoe-infected stand can lead to a very high degree of infection in the reproduction.

Theoretically mistletoe should be more amenable to control measures than many fungi. Mistletoe infections are confined to aerial parts of the tree, the "seeds" can not be carried along with the wind for any distance, and the parasite is killed with the death of the host, all of which are advantages, silviculturally, over most fungi. Complications arising from some logging practices have already been alluded to.

Also, control measures will have to be modified to suit the peculiarities of each species of mistletoe, some of which occur under quite different ecological conditions.

Many of the recommendations advanced for the management of mistletoe-infected forest stands can be applied to most species of the parasite. Silvicultural control methods must take into consideration the age of the stand concerned. For this purpose, Buckland and Marples (1952) offered the following suggestions for infected mature and overmature stands:

a) In clear-cutting, all residual trees and advanced reproduc-

tion should be destroyed. The clear-cut areas should be as large as can be allowed silviculturally.

b) When the block-system of cutting is used, mistletoe-infected blocks should be removed first.

c) If seed trees are to be left for reproductive purposes, they should be selected on their good form and apparent freedom from mistletoe.

For infected immature stands the following recommendations were given:

a) In any form of partial or selective cutting, all trees with mistletoe should be removed at the first cut, even to the extent of reducing the first cut to a non-profit operation.

b) Similarly, in any form of thinning, infected trees are to be removed first. An inspection, and removal of any infected trees previously overlooked, should be made no later than five years after the first treatment. This procedure was found to be sufficient to keep the parasite in check for all practical purposes (Anonymous, 1947).

When the infection concerns a relatively small part of the forest, it is feasible to stop the spread of the parasite by the establishment of a 60-foot mistletoe-free zone (Anonymous, 1949). In some of these cases, small timber sales or even free-use permits may be justified and effective (Weir, 1916*c*).

Working with *A. pusillum* on spruce, Anderson and Kaufert (1953) recognized a definite series of events in the development of an infection in an even-aged stand. The infection commonly starts in a small group of trees and slowly spreads outward, leaving the center of the infection in a state of destruction. The second generation in the vacated area is uneven-aged and heavily infected. The basis of the recommendations offered is the stage of development of the infection under consideration. In the initial stage, all broomed trees should be cut, as well as those within a zone of forty feet. In the second stage, when an opening, surrounded by broomed trees, is made in the canopy, the entire infected area plus a one-chain wide strip extending outward from the visibly broomed trees should be clear-cut. In this case, all spruce within this strip should be removed. In the later stage, a large area of ragged, uneven-aged and heavily infected trees is surrounded by a narrow zone of young reproduction and a belt of

broomed trees belonging to the original stand. To halt the advance of the mistletoe, the infected part of the surrounding stand plus a one-chain wide strip should be clear-cut immediately. Within this strip, all broomed merchantable trees should be cut, all non-merchantable trees either cut or pruned, This pruning treatment should include periodic repetition as described below.

Pruning methods are usually of little practical value in large-scale forest management but may be effective in small localities and in those where indivdual trees have high ornamental value, as on public camping grounds. Perry (1922) found a single pruning to be insufficient, since almost every tree developed mistletoe infections after pruning. The difficulty here lies in the fact that several years may be required for the germinating mistletoe plant to produce its first shoots. During this time the infection is practically invisible. If a pruning treatment is applied, therefore, it should be followed by a second treatment after the first mistletoe shoots have appeared of the infection thus hidden at the time of the first pruning, but before their production of fruits. It is unfortunate, for this reason, that data on the time elapsing between germination and the first flowering season for most species are not available. Also, the direction and rate of growth of the endophytic system are not accurately known (Gill, 1935). These gaps in our knowledge render any silvicultural treatment of dwarf mistletoes experimental. A recommendation to be kept in mind is that any such treatment, whether by logging or by pruning, should not be applied during the fruiting season (autumn), since the dispersal of " seeds " could be greatly assisted at this time.

Economic justification for any type of mistletoe control is naturally dependent on the value of the stand attacked. Mistletoe control procedures are at present rarely incorporated in silvicultural practices. Some trees attacked, such as western larch and white spruce, are not of great value as timber trees at localities of infection. It must be remembered, however, that the value of these trees quite possibly may go up to such an extent that control of their parasites will become necessary. In other trees, moreover, notably in western hemlock and Ponderosa pine, the damage due to mistletoe is of considerable magnitude and is liable to increase in succeeding generations unless more drastic measures are introduced (Gill, 1935).

OTHER CONTROLLING FACTORS

One of the least known facets of the study of *Arceuthobium* is that concerned with the background of its distribution. Discrepancies between the ranges of most species and those of their hosts exist but are as yet unexplained. The Douglas-fir mistletoe (*A. douglasii*) is common on its host in many places throughout the latter's range east of the Cascades. Yet it has not been found on the Pacific Coast Douglas-fir. The factors limiting the distribution of this parasite are in urgent need of study for very convincing reasons; the economic importance of Douglas-fir on the Pacific Coast is indisputable, and the introduction of mistletoe could possibly be disastrous.

Among factors controlling the spread of dwarf mistletoe might be mentioned the distance between clumps of trees or individual trees (von Schrenk, 1900); high winds, which in certain areas may serve as natural pruning agents, breaking off heavy brooms (Weir, 1916*a*); and finally, the effect of forest fires (Dowding, 1929; Roth, 1953). Dowding, working on *A. americanum* in Alberta, states categorically that fire is of prime importance in limiting the distribution of this parasite. She argues that the spread of mistletoe in an even-aged stand is so slow that the stand is usually destroyed by a forest fire before the infection becomes serious. In the writer's view, however, the controlling influence of fires could be of significance only in a limited sense. These forest fires are the chief factor through which the extensive lodgepole pine forests on the east slopes of the Rocky Mountains remain extant. If the areas would be completely protected from fires, the lodgepole pine would, in time, probably be succeeded by a spruce–alpine fir stand, in which *A. americanum* would not survive. In a much broader sense than Dowding's, therefore, forest fires maintain the range of *A. americanum*. Furthermore, a forest fire usually leaves certain remnants of the forest untouched, which, if originally infected, soon becomes virulent centers of dissemination because of improved light conditions.

RECIPROCAL LIST OF HOSTS AND PARASITES

In the following list, the nature of the reference within brackets is indicated by exponents: [1] is given to those cases where infection was brought about artificially, no natural records being availa-

ble;[2] is given to those records which are believed to be rare host-parasite relations. If a host-parasite combination is commonly found, no further exponent is used; similarly, if a combination is rare in nature, artificial infections are not mentioned. Authorities are stated for parasites in the first, for hosts in the second section, only. In selecting references, those most complete, in the writer's opinion, were given preference.

By Parasite

[1]: artificially only; [2]: rarely

A. americanum Nutt. ex. Engelm.

Picea glauca[2]	(Bourchier and Kuijt, 1953)
Pinus albicaulis[2]	(Gill, 1935)
P. attenuata[2]	(Gill, 1935)
P. banksiana	(Gill, 1935)
P. contorta	(Gill, 1935)
P. edulis[2]	(Gill, 1935)
P. flexilis[2]	(Gill, 1935)
P. jeffreyi[2]	(Gill, 1935)
P. montana[1]	(Weir, 1918*b*)
P. ponderosa[2]	(Gill, 1935)

A. campylopodum Engelm.

Pinus muricata	(Howell, 1949)
P. occidentalis ?	(Urban, 1912)

A. campylopodum Engelm. f. *abietinum* (Engelm.) Gill

Abies amabilis[2]	(Gill, 1935)
A. arizonica[2]	(Gill, 1935)
A. concolor	(Gill, 1935)
A. grandis[2]	(Gill, 1935)
A. lasiocarpa[2]	(Gill, 1935)
A. magnifica	(Gill, 1935)
A. procera	(Gill, 1935)
A. shastensis	(Hedgcock, 1915)

f. *blumeri* (A. Nelson) Gill

Pinus lambertiana	(Gill, 1935)
P. monticola[2]	(Gill, 1935)
P. reflexa	(Gill, 1935)

f. *campylopodum* (Engelm.) Gill

Abies concolor [1]	(Weir, 1918*a*)
A. grandis [1]	(Weir, 1918*a*)
Larix europaea [1]	(Weir, 1918*a*)
L. occidentalis [1]	(Weir, 1918*a*)
Picea excelsa [1]	(Weir, 1918*a*)
Pinus attenuata	(Gill, 1935)
P. banksiana [1]	(Hedgcock and Hunt, 1917)
P. bungeana [1]	(Hedgcock and Hunt, 1917)
P. caribea [1]	(Hedgcock and Hunt, 1917)
P. contorta	(Gill, 1935)
P. coulteri	(Gill, 1935)
P. jeffreyi	(Gill, 1935)
P. montana [1]	(Weir, 1918*a*)
P. pinea [1]	(Hedgcock and Hunt, 1917)
P. ponderosa	(Gill, 1935)
P. radiata	(Gill, 1935)
P. resinosa [1]	(Weir, 1918*a*)
P. sabiniana	(Gill, 1935)
P. sylvestris [1]	(Weir, 1918*a*)
P. virginiana [1]	(Hedgcock and Hunt, 1917)
	f. *cyanocarpum* (A. Nelson) Gill
Pinus albicaulis [2]	(Gill, 1935)
P. aristata [2]	(Gill, 1935)
P. balfouriana [2]	(Gill, 1935)
P. flexilis	(Gill, 1935)
	f. *divaricatum* (Engelm.) Gill
Pinus cembroides	(Gill, 1935)
P. edulis	(Gill, 1935)
P. monophylla	(Gill, 1935)
P. parryana	(Gill, 1935)
	f. *laricis* (Piper) Gill
Abies grandis [1]	(Weir, 1918*a*)
A. lasiocarpa [2]	(Weir, 1918*c*)
Larix europaea [1]	(Weir, 1918*a*)

L. leptolepis [1]	(Weir, 1918*a*)
L. lyallii	(Gill, 1935)
L. occidentalis	(Gill, 1935)
Picea engelmanni [2]	(Weir, 1918*c*)
Pinus albicaulis [2]	(Weir, 1918*c*)
P. contorta [2]	(Weir, 1918*c*)
P. monticola [2]	(Kuijt, 1953)
P. ponderosa [2]	(Weir, 1918*a*)
f. *microcarpum* (Engelm.) Gill	
Picea breweriana [2]	(Gill, 1935)
P. engelmanni [2]	(Gill, 1935)
P. pungens [2]	(Gill, 1935)
f. *tsugensis* (Rosend.) Gill	
Abies lasiocarpa [1]	(Weir, 1918*a*)
Tsuga canadensis [1]	(Weir, 1918*a*)
T. heterophylla	(Gill, 1935)
T. mertensiana	(Gill, 1935)
A. chinense Lec.	
Abies sp.	(Lecomte, 1915)
Keteleeria sp.	(Handel-Mazetti, 1929)
Pinus tabulaeformis	(Handel-Mazetti, 1929)
A. douglasii Engelm.	
Abies concolor [2]	(Hawksworth, 1952)
A. grandis [2]	(Weir, 1918*c*)
A. lasiocarpa [1]	(Weir, 1918*a*)
Picea engelmanni [2]	(Weir, 1918*c*)
Pseudotsuga macrocarpa	(Jepson, 1923)
P. menziesii	(Gill, 1935)
A. minutissimum Hook. f.	
Pinus excelsa	(Hooker, 1886)
A. oxycedri (DC.) Bieb.	
Chamaecyparis sphaeroidea [1]	(Heinricher, 1930)
Cupressus sp.[1]	(Heinricher, 1920)
Juniperus brevifolia	(Turrill, 1920)
J. communis	(Turrill, 1920)
J. drupacea	(Turrill, 1920)
J. excelsa	(Komarov, 1936)

J. oxycedrus	(Turrill, 1920)
J. phoenicea	(Turrill, 1920)
J. procera	(Turrill, 1920)
J. rufescens	(Turrill, 1920)
J. sabina	(Turrill, 1920)
J. semiglobosa	(Komarov, 1936)
J. seravschanica	(Komarov, 1936)
J. turcomanica	(Komarov, 1936)
A. pusillum Peck	
Larix laricina [2]	(Jones, 1900)
Picea glauca	(Gill, 1935)
P. mariana	(Gill, 1935)
P. rubens	(Gill, 1935)
Pinus banksiana [2]	(Pomerleau, 1941)
P. resinosa [2] *	.....
P. strobus [2]	(House, 1935)
A. vaginatum (Willd.) Presl	
Abies religiosa	(Gill, 1935)
Pinus arizonica	(Gill, 1935)
P. chihuahuana	(Hedgcock, 1915)
P. hartwegii	(Roldan, 1924)
P. jeffreyi	(Rydberg, 1917)
P. latifolia	(Gill, 1935)
P. leiophylla	(Gill, 1935)
P. ponderosa	(Gill, 1935)
P. tenuifolia †	.....

By Host

Abies amabilis (Dougl.) Forbes	
A. campylopodum f. *abietinum* [2]	(Gill, 1935)
Abies arizonica Merr.	
A. campylopodum f. *abietinum* [2]	(Gill, 1935)
Abies concolor Lindl. & Gord.	
A. campylopodum f. *abietinum*	(Gill, 1935)
f. *campylopodum* [1]	(Weir, 1918*a*)
f. *laricis* [1]	(Weir, 1918*a*)
A. douglasii [2]	(Weir, 1918*c*)

* Specimen in Herbarium, University of Toronto, Ontario. Courtesy Mr. W. G. Ziller.

† Specimen in Herbarium, University of California, Berkeley, California.

Abies lasiocarpa (Hook.) Nutt.	
A. campylopodum f. *abietinum* [2]	(Gill, 1935)
f. *laricis* [2]	(Weir, 1918*c*)
f. *tsugensis* [1]	(Weir, 1918*a*)
A. douglasii [1]	(Weir, 1918*a*)
Abies magnifica Murr.	
A. campylopodum f. *abietinum*	(Gill, 1935)
Abies procera Rehder	
A. campylopodum f. *abietinum*	(Gill, 1935)
Abies religiosa Lindl.	
A. vaginatum	(Gill, 1935)
Abies shastensis Lemmon	
A. campylopodum f. *abietinum* [2]	(Hedgcock, 1915)
Abies sp.	
A. chinense	(Lecomte, 1915)
Chamaecyparis sphaeroidea Spach	
A. oxycedri [1]	(Heinricher, 1930)
Cupressus sp.	
A. oxycedri [1]	(Heinricher, 1920)
Juniperus brevifolia Ant.	
A. oxycedri	(Turrill, 1920)
Juniperus communis L.	
A. oxycedri	(Turrill, 1920)
Juniperus drupacea Labill.	
A. oxycedri	(Turrill, 1920)
Juniperus excelsa Bieb.	
A. oxycedri	(Komarov, 1936)
Juniperus oxycedrus L.	
A. oxycedri	(Turrill, 1920)
Juniperus phoenicea L.	
A. oxycedri	(Turrill, 1920)
Juniperus procera Hochst. ex Endl.	
A. oxycedri	(Turrill, 1920)
Juniperus rufescens Link	
A. oxycedri	(Turrill, 1920)
Juniperus sabina L.	
A. oxycedri	(Turrill, 1920)
Juniperus semiglobosa Regel	
A. oxycedri	(Komarov, 1936)

Juniperus seravschanica Komar.	
A. oxycedri	(Komarov, 1936)
Juniperus turcomanica Fedtsch.	
A. oxycedri	(Komarov, 1936)
Keteleeria sp.	
A. chinense	(Handel-Mazetti, 1929)
Larix europaea DC.	
A. campylopodum f. *campylopodum* [1]	(Weir, 1918*a*)
f. *laricis* [1]	(Weir, 1918*a*)
Larix laricina (Du Roi) Koch	
A. pusillum [2]	(Jones, 1900)
Larix leptolepis Hort. ex Endl.	
A. campylopodum f. *laricis* [1]	(Weir, 1918*a*)
Larix lyallii Parl.	
A. campylopodum f. *laricis*	(Gill, 1935)
Larix occidentalis Nutt.	
A. campylopodum f. *campylopodum* [1]	(Weir, 1918*a*)
f. *laricis*	(Gill, 1935)
Picea breweriana Watson	
A. campylopodum f. *microcarpum* [2]	(Gill, 1935)
Picea engelmanni Parry	
A. campylopodum f. *microcarpum* [2]	(Gill, 1935)
f. *laricis* [2]	(Weir, 1918*c*)
A. douglasii [2]	(Weir, 1918*c*)
Picea excelsa Link	
A. campylopodum f. *campylopodum* [1]	(Weir, 1918*a*)
Picea glauca (Moench) Voss	
A. americanum [2]	(Bourchier and Kuijt, 1953)
A. pusillum	(Gill, 1935)
Picea mariana (Mill.) B. S. P.	
A. pusillum	(Gill, 1935)
Picea pungens Engelm.	
A. campylopodum f. *microcarpum* [2]	(Gill, 1935)
Picea rubens Sarg.	
A. pusillum	(Gill, 1935)
Pinus albicaulis Engelm.	
A. americanum [2]	(Gill, 1935)

A. campylopodum f. *cyanocarpum* [2]	(Gill, 1935)
f. *laricis* [2]	(Weir, 1918*c*)
Pinus aristata Engelm.	
A. campylopodum f. *cyanocarpum* [2]	(Gill, 1935)
Pinus arizonica Engelm.	
A. vaginatum	(Gill, 1935)
Pinus attenuata Lemmon	
A. americanum [2]	(Gill, 1935)
A. campylopodum f. *campylopodum*	(Gill, 1935)
Pinus balfouriana Jeffrey ex Murray	
A. campylopodum f. *cyanocarpum* [2]	(Gill, 1935)
Pinus banksiana Lamb.	
A. americanum	(Gill, 1935)
A. campylopodum f. *campylopodum* [1]	(Hedgcock and Hunt, 1917)
A. pusillum [2]	(Pomerleau, 1941)
Pinus bungeana Zucc.	
A. campylopodum f. *campylopodum* [1]	(Hedgcock and Hunt, 1917)
Pinus cembroides Gord.	
A. campylopodum f. *divaricatum*	(Gill, 1935)
Pinus chihuahuana Engelm.	
A. vaginatum	(Hedgcock, 1915)
Pinus contorta Dougl. ex Loud.	
A. americanum	(Gill, 1935)
A. campylopodum f. *campylopodum*	(Gill, 1935)
f. *laricis* [2]	(Weir, 1918*c*)
Pinus coulteri Don.	
A. campylopodum f. *campylopodum*	(Gill, 1935)
Pinus edulis Engelm.	
A. americanum [2]	(Gill, 1935)
A. campylopodum f. *divaricatum*	(Gill, 1935)
Pinus excelsa Wall. ex Lamb.	
A. minutissimum	(Hooker, 1886)
Pinus flexilis James	
A. americanum [2]	(Gill, 1935)
A. campylopodum f. *cyanocarpum*	(Gill, 1935)
Pinus hartwegii Lindl.	
A. vaginatum	(Roldan, 1924)

Pinus jeffreyi Murr.	
A. americanum [2]	(Gill, 1935)
A. campylopodum f. *campylopodum*	(Gill, 1935)
A. vaginatum	(Gill, 1935)
Pinus latifolia Sarg.	
A. vaginatum	(Gill, 1935)
Pinus lambertiana Dougl.	
A. campylopodum f. *blumeri*	(Gill, 1935)
Pinus leiophylla Schlecht. & Cham.	
A. vaginatum	(Gill, 1935)
Pinus monophylla Torr. & Frém.	
A. campylopodum f. *divaricatum*	(Gill, 1935)
Pinus montana Mill.	
A. americanum [1]	(Weir, 1918*b*)
A. campylopodum f. *campylopodum* [1]	(Weir, 1918*b*)
Pinus monticola Dougl. ex Lamb.	
A. campylopodum f. *blumeri* [2]	(Gill, 1935)
f. *laricis* [2]	(Kuijt, 1953)
Pinus muricata Don.	
A. campylopodum	(Howell, 1949)
Pinus occidentalis Sw.	
A. campylopodum ?	(Urban, 1912)
Pinus parryana Engelm.	
A. campylopodum f. *divaricatum*	(Gill, 1935)
Pinus pinea L.	
A. campylopodum f. *campylopodum* [1]	(Hedgcock and Hunt, 1917)
Pinus ponderosa Dougl. ex Laws.	
A. americanum [2]	(Gill, 1935)
A. campylopodum f. *campylopodum*	(Gill, 1935)
f. *laricis* [2]	(Weir, 1918*a*)
A. vaginatum	(Gill, 1935)
Pinus radiata Don.	
A. campylopodum f. *campylopodum*	(Gill, 1935)
Pinus resinosa Ait.	
A. campylopodum f. *campylopodum* [1]	(Weir, 1918*a*)
A. pusillum [2]	(See footnote *, p. 606)
Pinus sabiniana Dougl.	
A. campylopodum f. *campylopodum*	(Gill, 1935)

Pinus reflexa (Engelm.) Engelm.	
A. campylopodum f. *blumeri* [2]	(Gill, 1935)
Pinus strobus L.	
A. pusillum [2]	(House, 1935)
Pinus sylvestris L.	
A. campylopodum f. *campylopodum* [1]	(Weir, 1918*a*)
Pinus tabulaeformis Hort. ex Carr.	
A. chinense	(Handel-Mazetti, 1929)
Pinus tenuifolia Benth.	
A. vaginatum	(See footnote †, p. 606)
Pinus virginiana Mill.	
A. campylopodum f. *campylopodum* [1]	(Hedgcock and Hunt, 1917)
Pseudotsuga macrocarpa (Torr.) Mayr.	
A. douglasii	(Jepson, 1923)
Pseudotsuga menziesii (Mirb.) Franco	
A. douglasii	(Gill, 1935)
Tsuga canadensis (L.) Carr.	
A. campylopodum f. *tsugensis* [1]	(Weir, 1918*a*)
Tsuga heterophylla (Raf.) Sarg.	
A. campylopodum f. *tsugensis*	(Gill, 1935)
Tsuga mertensiana (Bong.) Sarg.	
A. campylopodum f. *tsugensis*	(Gill, 1935)

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Male shoot and flowers.
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ACKNOWLEDGEMENTS

The writer wishes to express his sincere appreciation to Dr. T. M. C. Taylor, Department of Biology and Botany, University of British Columbia, Vancouver, for his many valuable suggestions and guidance throughout the review; to Dr. V. J. Nordin, Officer-in-Charge, Forest Pathology Laboratory, Calgary, for his assistance in the preparation of this report; and to various members of his staff, in particular to Miss J. Hewitt, for the preparation of the photographic plates. A word of thanks is also due to Dr. Adriance S. Foster, University of California at Berkeley, for criticizing the revised section on the endophytic system.

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PLATE I

Common Host-Parasite Associations

FIG. 1. *Arceuthobium americanum* (male) on *Pinus contorta*. Kananaskis, Alberta. Ca. × 1.

FIG. 2. *A. campylopodum* f. *tsugensis* (male) on *Tsuga heterophylla*. Vancouver, B. C. Ca. × ½.

FIG. 3. *A. douglasii* (male) on *Pseudotsuga taxifolia*. Kootenay Lake, B. C. Ca. × 1.

FIG. 4. *A. campylopodum* f. *laricis* (female) on *Larix occidentalis*. St. Mary's Lake, B. C. Ca. × 1.

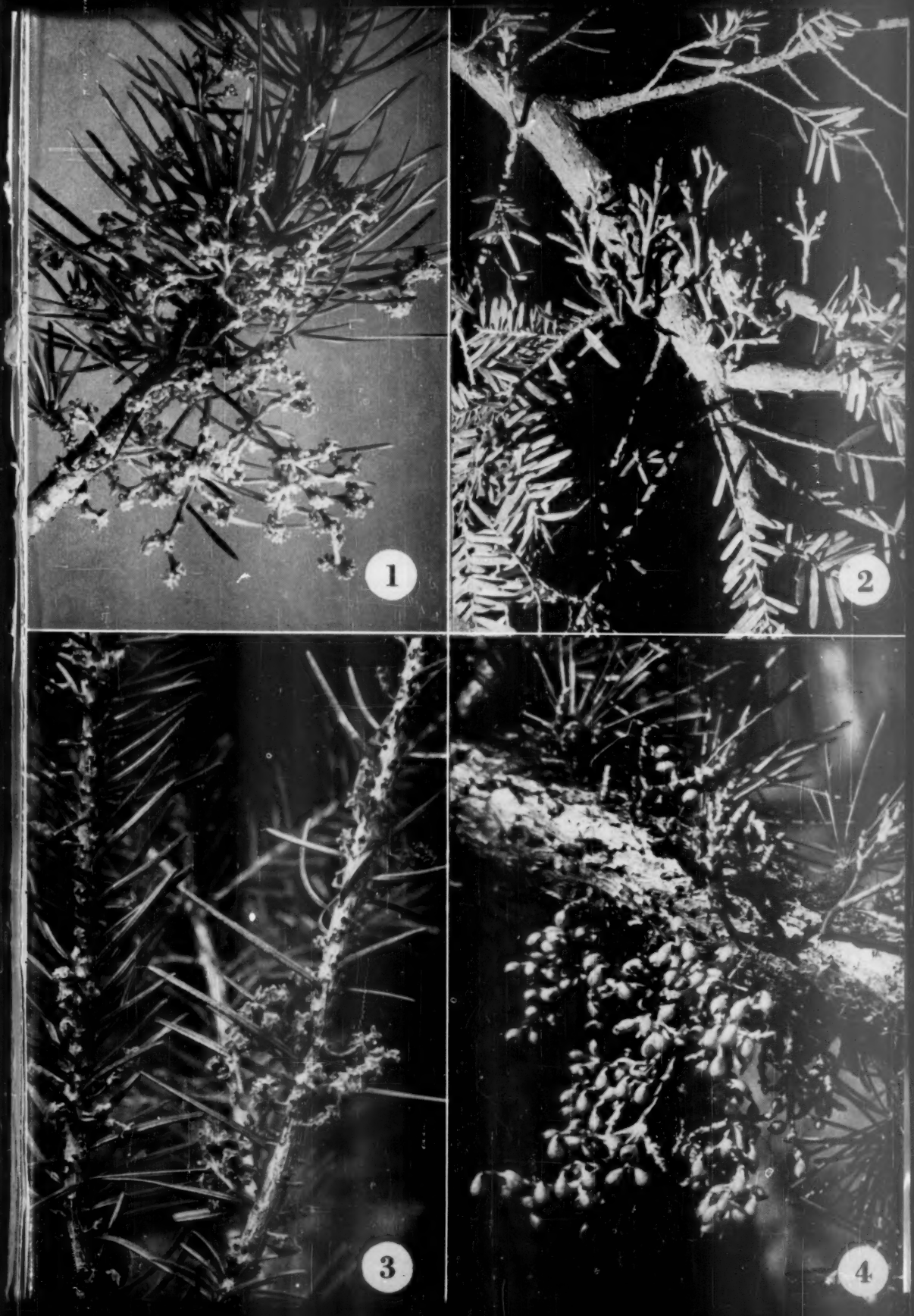
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PLATE II

Unusual Host-Parasite Associations

FIG. 5. *Arceuthobium americanum* (female) on *Picea glauca*. Kananaskis, Alberta. Ca. × 2.

FIG. 6. *A. campylopodum* f. *laricis* (male) on *Pinus contorta*. Christina Lake, B. C. Ca. × 1.

FIG. 7. *A. campylopodum* f. *laricis* (male) on *Pinus monticola*. Slocan Lake, B. C. Ca. × ½.

FIG. 8. *A. campylopodum* f. *laricis*, (female) on *Pinus monticola*. Slocan Lake, B. C. Ca. × 1.

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PLATE III

Witches' Brooms

FIG. 9. *Arceuthobium americanum* on *Pinus ponderosa*. Kimberley, B. C.
FIG. 10. *A. americanum* on *Picea glauca*. Kananaskis, Alberta.
FIG. 11. *A. americanum* on *Pinus banksiana*. Calling Lake, Alberta.
FIG. 12. *A. americanum* on *Pinus contorta*. Banff, Alberta.

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PLATE IV

Witches' Brooms (*Continued*)

FIG. 13. *Arceuthobium campylopodum* f. *laricis* on *Larix occidentalis*. St. Mary's Lake, B. C.

FIG. 14. *A. douglasii* on *Pseudotsuga taxifolia*. Kootenay Lake, B. C.

Hyperparasitism

FIG. 15. *Wallrothiella arceuthobii*, parasitic on berries of a female colony of *A. americanum* on *Pinus contorta*. Kootenay National Park, B. C. Ca. × 1.

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